

A NEW CEPHALOPOD FAUNA FROM THE LOWER CARBONIFEROUS OF EAST CORNWALL

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ABSTRACT. A collection of approximately three hundred small cephalopods from a site in the Lower Carboniferous of east Cornwall includes representatives of *Gattendorfia* sp., Gen. et sp. nov. A, *Muensteroceras complanatum*, M. cf. *rotella*, *Ammonellipsites princeps*, A. sp. aff. *asiaticus*, A. sp. indet. and Gen. et sp. nov. B. It is argued that the fauna is of an age later than those of the Hangenbergkalk ('cul') of Germany and possibly earlier than the late Tournaisian cephalopods of Belgium ('culIa'). German conodont evidence, taken together with some from Belgium, demonstrates that there is a range of Tournaisian age (Tn 2a-Tn 3b? in terms of the Belgian stratigraphy, or approximately the *Siphonodella crenulata* Zone in terms of conodonts) of which the cephalopod-based zonal standard makes no account. Certain North American (Mississippian) cephalopod faunas which show coincidences of cheilocerataean (including gattendorfiid) and goniatitacean (including muensteroceratid and ammonellipsitid) forms have not found accommodation in the European zonal scheme. In the cases of the Chouteau limestone, Rockford limestone, and Walls Ferry limestone the evidence of conodonts suggests reference to that range of the Tournaisian where the European cephalopod standard fails.

CEPHALOPODS occur only rarely in successions of early Carboniferous age. The zonal scheme based on these fossils can be no better than the patchy record allows. So, too, with matters of phylogeny: any discussion of the emergence of the goniatitaceans (eventually the dominant group of Carboniferous goniatites) is hindered by the poverty of the evidence at present available. In these circumstances a certain degree of interest attaches to a new fauna which appears to be of Tournaisian age and which has, as contemporaries, cheilocerataean and goniatitacean forms.

This paper is concerned mainly with the question of the age of the fauna as indicated by the most nearly mature goniatites present. A later communication will refer to the detail of immature forms and to ontogenies, and will review the current state of information on Tournaisian goniatites.

THE NEW FAUNA FROM EAST CORNWALL

A detached sheet of Lower Carboniferous rocks forms the mass of Viverdon Down south and east of Callington in east Cornwall. It emerged during mapping that the sheet includes a lower succession in which shales are predominant and an upper which has the tougher, siliceous rocks that define the topographic high. The lower succession is exposed at SX 398665 in a cutting on the narrow road which leads south-eastward down to the Tamar at Haltonquay. On the south-western side of the road thin cross-stratified siltstones occur among the dark shales, and at the north-western end of the exposure, near to the entrance to Heathfield Farm, coarse sandstones are exposed. These are taken to be associated with the finer-grained rocks in the stratigraphy of the lower part of the detached sheet. At a point approximately 30 metres south-east of the entrance to Heathfield Farm, and 2½ m. above the present road level in the cutting, there is a lens of iron-shot, relatively coarse material disposed parallel to bedding within the shale and siltstone succession. When first discovered the remnant of the lens measured approximately

60 cm. by 4 cm. as exposed on the weathered face, and it proved to continue for 10 cm. maximum in the third dimension. Only the last 'tail' of the lens now remains in the exposure. Small cephalopods were visible on the site, and later preparation (under the microscope, with needle and brush) finally freed over three hundred individual fossils. Only molluscs are recognizable, and the minority of these are minute. There are no conodonts.

COMMENTS ON SIZE, AND ON BURIAL AND PRESERVATION

The range of size of the goniatites is shown in text-fig. 1. The smaller forms can be allotted to genera by continuous association of details of form down through the size-range. The graph of sizes of the generically indeterminable goniatites illustrates the obvious fact that the smallest individuals present the greatest difficulties of identification. Representatives of the ribbed ammonellipsitids and of Gen. et sp. nov. B, which is keeled at all growth stages, can nevertheless be confidently identified down to values of diameter in the neighbourhood of 1 mm. The size-frequency of all goniatites collected peaks at the 1-2 mm. grade.

There are many specimens in which living chamber and gas chambers can be distinguished. They indicate that the smallness of the fossils cannot be due to breakage during a transport-burial sequence of events or during preparation. Nor is this the kind of preservation in which only nuclei survive diagenesis in a robust state. In a majority of cases the fossils represent the stage of growth achieved at the time of death. The range of size and the range of form (evolute near-serpenticones to tightly involute near-cadicones, and orthocones and small, low-turreted gastropods are also present, if rare) suggest that this close concentration of such diverse individuals cannot have experienced any lengthy exposure to a sorting process.

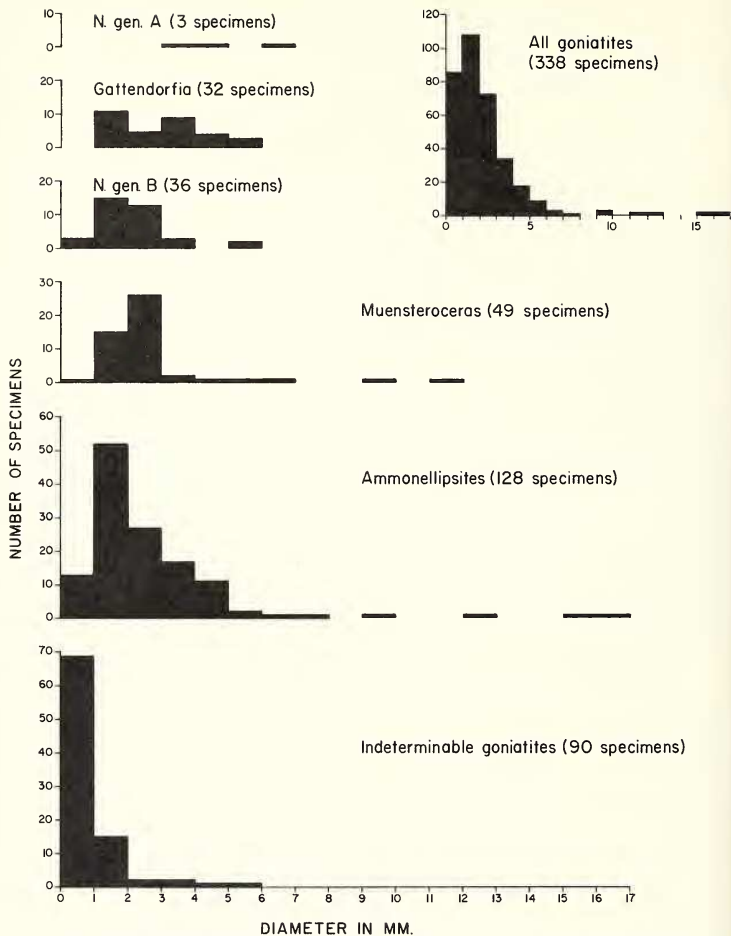
The fossils are found silicified in a lens which is cut by many small siliceous veins. The more general silicification which affects the immediately higher part of the stratigraphy is, however, not developed here.

THE FAUNA AND ITS AGE

The following are identified:

- Gattendorfia* sp.
- Gen. et sp. nov. A
- Muensteroceras complanatum* (de Koninck)
- Muensteroceras* cf. *rotella* (de Koninck)
- Muensteroceras* spp.
- Ammonellipsites princeps* (de Koninck)
- Ammonellipsites* sp. aff. *asiaticus* (Librovitch)
- Ammonellipsites* sp. indet.
- Ammonellipsites* spp.
- Gen. et sp. nov. B

Indeterminable low-spined gastropods and small orthocones are also present.



TEXT-FIG. 1. Size distribution of goniatites in the new fauna from Cornwall, by genera and (top right) for all goniatites collected.

The occurrence is stratigraphically in isolation. The nearest occurrence of any other fossils is at a point 800 m. to the west and some 100 m. higher in the succession (as judged from a map) where conodonts of the *anchoralis*-Zone are found (Matthews 1969a).

The cephalopods include *Ammonellites princeps* and *Muensteroceras complanatum*, and these are the indices to the first of the units ($\text{cuII}\alpha$) distinguished by Schmidt (1925) in the *Pericyclus*-Stufe (cuII , now the *Ammonellites*-Stufe—see Paproth, Teichmüller, and Remy 1960). But the Belgian original has been, until now, the sole western European occurrence of these forms, and it is therefore difficult to arrive at any understanding of stratigraphic limits for $\text{cuII}\alpha$. Also, the new fauna from Cornwall shows these two forms in an association altogether different from that found in Belgium (Delépine 1940a). For these reasons it becomes necessary to examine the composition of the currently accepted zonal scheme (which is in most essentials that advanced by Schmidt in 1925) in order to discover the constraints that exist in the matter of judging the age of the new fauna.

The cephalopod-based standard includes, in the Lower Carboniferous, three stages, successively the *Gattendorfia*-Stufe (cuI), *Ammonellites*-Stufe (cuII), and *Goniatites*-Stufe (cuIII). Schmidt's contribution of 1925 offered more detailed proposals than had been available before on the succession of faunas in cuII and cuIII and (this as a complete novelty) cuI subjoined to the two Lower Carboniferous stages previously recognized. Schindewolf (1927) would have preferred to define the beginning of the Carboniferous by reference to the entry of the distinctively Carboniferous goniatitaceans, with a median saddle as their characteristic. Schmidt was guided by altogether a different consideration. He brought forward the *Gattendorfia*-Stufe (then known as the *Protocanites*-Stufe) as the earliest Carboniferous unit because field mapping, particularly the work of Paeckelmann (1922), had indicated that the *Protocanites*-Stufe stratigraphy might be regarded as an equivalent of the Étroeungt. More recently, Vöhringer (1960) has presented a detailed analysis of the stratigraphic distribution, form and phylogenetic relationships of the cephalopods that occur in the 2 m. thick Hangenbergkalk, the type example of cuI . Vöhringer retained the definition of the lower limit of the Carboniferous as the point of entry of *Gattendorfia subinvoluta*, and added clarification by showing that *Balvia* is an imitoceratid. However, for want of any information from the stratigraphy above the Hangenbergkalk (the Liegende Alaunschiefer) he was unable to propose any upper limit to cuI . Among his cephalopods there was an example of *Karagandoceras*, a genus which possesses a median saddle, but which according to Vöhringer should be regarded as precocious in this respect, and should not be identified as the first of the major suite of goniatitaceans. Weyer (1965) has restudied the collections of *Gattendorfia*-Stufe material from Dzikowiec (Ebersdorf) in Lower Silesia, and has been able to suggest that *Paralytoceras*, too, anticipates later forms in its possession of a median saddle.

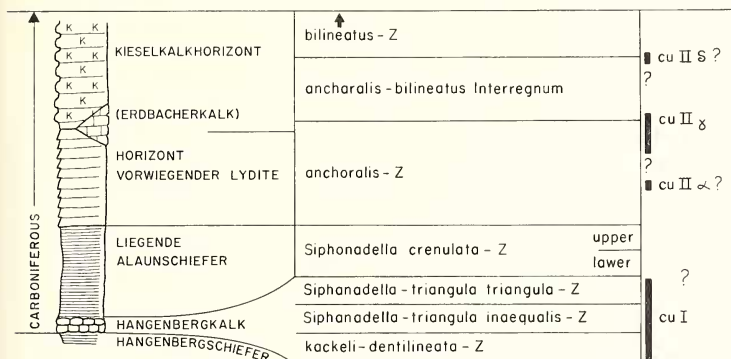
Schmidt's *Ammonellites*-Stufe units, $\text{cuII}\alpha$, β , γ , δ , were founded on occurrences of cephalopods in respectively Belgium, Ireland, Germany (Dillmulde), and Germany (Harz). In the case of $\text{cuII}\alpha$, the material comes from the Calcaire de Vaux-Calcaire de Calonne range of the stratigraphy according to Delépine (1940a). In Legrand, Mamet, and Mortelmans (1966) the site is referred to Tn 3c. The Irish $\text{cuII}\beta$ forms (Foord 1903) cannot be given any exact stratigraphic attribution. The Erdbacherkalk, the $\text{II}\gamma$ type (Holzapfel 1889, Schmidt 1925) rests on pillow lavas. Its local stratigraphical relationships

and its content of reworked Upper Devonian conodonts have been described by Walliser and others (1958) and by Krebs (1963). The original occurrence of the cuII δ fauna (Schmidt 1941) was in a bed of red shale, a few centimetres thick, which outcrops near Riefensbeek in the Harz Mountains. Plainly, there is no possibility of guaranteeing the cuI-cuII relationship nor the interrelationships of the cuII units by direct observation of stratigraphic superpositions. Only in the case of the cuII-cuIII transition can this be done, for the cuII δ horizon, with *Entogonites nasutus*, has now been identified in the Rheinisches Schiefergebirge and its stratigraphic relationship to the cuIII α marker horizons demonstrated (Nicolaus 1963). Schmidt's scheme of zones of 1925 had to depend on a presumed course of phylogenesis (based mainly on the sequence of prolecanitids) supported at one point by Belgian evidence taken to confirm the relative age of cuII α and cuII γ . The scheme has been available for over forty years. It can be seen to be weak in that it was based on evidence from a relatively small number of scattered localities. It has survived, free from any serious challenge, because of the continuing poverty of the evidence. But there have been occasional finds of cephalopod faunas which could not satisfactorily be dated by reference to this standard. Notable European examples are those from Zadzelsdorf (Schindewolf 1922, 1926, 1939) and Iberg-Winterberg (Schindewolf 1951a). The early Mississippian goniatite faunas of the U.S.A. likewise have never found accommodation in Schmidt's scheme.

An alternative means of dating rock-successions of this range of age has appeared by the development in recent years of a zonal scheme based on conodonts. Voges's (1959, 1960) proposals, now confirmed and further elaborated by Meischner (in press), are based on detailed collecting from continuous sections. That information includes some obtained from sites where cephalopods occur, such as the Hangenbergkalk and the Erdbacherkalk. In 1960, Voges attempted a reconciliation of the two schemes. He claimed that cuII α and cuII β were distinguishable from one another (and referred especially to Delépine's (1940b) treatment of Irish faunas) but that cuII β and cuII γ were not. His tentative proposal was that the *Siphonodella crenulata* Zone should be equated with cuII α , and the *anchoralis* Zone with cuII β / γ . It should be understood that neither cuII α nor cuII β were identifiable in the sections from which his conodonts came, and also that the *anchoralis* Zone (as Voges himself showed) does not extend to the top of the Erdbacherkalk, the cuII γ type. On the other hand, his proposals for cuI units, based on the evidence of the Hangenbergkalk, are irrefragable.

It is now possible to use conodonts as a means of distinguishing Belgian equivalents of the German stratigraphic units, and the results are immediately of relevance here. Conil, Lys, and Mauvier (1964) produced a preliminary account of the conodonts they had discovered in the Franco-Belgian Lower Carboniferous. As Paproth (1964) has pointed out, this made it possible to recognize Tn 1b as the Hangenbergkalk correlative. It follows that some hundreds of metres of the Belgian succession (Legrand, Mamet, and Mortelmans 1966) intervene between the cuI horizon and the cuII α source. This range is unrecognized in the statement of cephalopod zones. In terms of conodonts it is approximately the *Siphonodella crenulata* Zone of Voges. Further, Conil, Lys, and Mauvier's discovery of *Scaliognathus anchoralis* in Tn 3c indicates that the cuII α source lies within Voges's *anchoralis* Zone, and consequently that Voges was mistaken in his tentative equation of the *anchoralis* Zone with cuII β / γ . A new rendering of relationships linking cephalopod occurrences and conodont zones is offered in text-fig. 2.

The Hangenbergkalk record of cephalopods fails to close with that from the late Tournaisian of Belgium and the cephalopod zonal scheme is seen to be discontinuous. In the past it has been suggested that the sufficiency of the scheme was confirmed by the work of Librovitch (1940), who dealt with an unusually rich body of material from



TEXT-FIG. 2. Rock-units in the Lower Carboniferous stratigraphy of Germany, and the conodont-zones established there (after Voges). Standard cephalopod occurrences may be referred to the conodont scheme as suggested on the right of the diagram.

Kazakhstan. Librovitch proposed a succession of 'faunal complexes' which appeared to repeat the sequence of stages proposed by Schmidt in 1925. The complexes do not, however, stand as independent confirmation of the standard scheme. They were modelled on the existing western European proposals, as Librovitch himself plainly admitted.

The new fauna from Cornwall may be of *Siphonodella crenulata*-Zone age, certainly later than the Hangenbergkalk faunas, possibly earlier than those of the late Tournaisian of Belgium in that there is coincidence of *Gattendorfia* and *Anmonellipsites*. This estimate of the age relative to Tn 3c is not easily made. *Anmonellipsites princeps* and *Muensteroceras complanatum* are common to the two. The new elements in the Cornish fauna, since they are unique to this case, have no part in a question of relative age. The mere presence of gattendorfiids has no immediate significance, for an argument of age based on late survival is never entirely satisfactory. But the gattendorfiids seen here resemble the small, slightly more evolute, constricted '*Kazakhstania*?' of the Walls Ferry limestone of Arkansas (see below) and in this there is an indirect suggestion that the Cornish fauna might predate Tn 3c. The fauna adds to the record of Tournaisian goniatites, and it may have its place within the gap now seen to interrupt the standard sequence of zones; but it does not by any means close that gap nor provide any justification for proposing a new zone.

The view that a coincidence of gattendorfiid and goniatite cephalopods exists in a post-Hangenbergkalk, pre-Calcaire de Calonne range of age is strongly encouraged

by the American evidence. It is necessary to refer here to the conodonts of the *Siphonodella quadruplicata*-*S. crenulata* Zone and of the *Siphonodella isosticha*-*S. cooperi* Zone. These may be equated with European proposals as is done in Canis (1968, table 2), but neither should be regarded as identifying $cuII_{\alpha}$. Also, it should be noted that the *Siphonodella isosticha*-*S. cooperi* Zone can be found to precede the *anchoralis* Zone in Europe (Matthews 1969b). The Chouteau limestone, according to Miller and Collinson (1951), produces representatives of the following cephalopod genera: *Gattendorfia*, *Muensteroceras*, *Ammonellipsites*, *Imitoceras*, *Protocanites*, and *Prodromites*. Canis (1968) refers the Chouteau limestone to the *S. quadruplicata*-*S. crenulata* and *S. isosticha*-*S. cooperi* Zones. The Rockford limestone of Indiana has, at the type locality, *Imitoceras*, *Muensteroceras*, *Protocanites*, and *Prodromites* (Miller and Collinson 1951) and has produced a *Gattendorfia* species in north-western Indiana (Gutschick and Treckmann 1957). Rexroad and Scott (1964) report that the Rockford limestone has the conodonts of the *S. isosticha*-*S. cooperi* and *Gnathodus semiglaber*-*Pseudopolygnathus multistriata* Zones. Gordon (1964) lists *Gattendorfia*, '*Kazakhstania*?', *Ammonellipsites*, and *Muensteroceras* from the Walls Ferry limestone of Arkansas and observes that conodonts, dominated by siphonodellids (according to W. H. Hass), are found in a bed which lies 1 ft. below the cephalopod occurrence. Gordon (1964) reports too the existence of a *Gattendorfia* specimen from the lower part of the Lodgepole limestone of Montana and an ammonellipsitid, as yet undescribed, again from the Lodgepole. Klapper (1966) has described conodonts of the 'lower *Siphonodella crenulata* Zone' (which, misled by German practice, he equates with $cuII_{\alpha}$) from the basal part of the Lodgepole.

The record of American information is not as full as might be desired. For example, it would be preferable to identify the exact stratigraphic provenance of cephalopod material and to refer in every case to conodont material taken from the same horizon. Again, greater fullness is desirable in that the outstanding 'misfit' (as seen from Europe), the Marshall sandstone fauna of Michigan, cannot yet be referred to a conodont-based age-standard. But the evidence so far available may be sufficient to show that there is little purpose in attempting to judge the age of these early Mississippian faunas by reference to the European scheme of cephalopod zones. They appear to belong to a range of age which goes unregarded in the cephalopod scheme and which can be distinguished only by the evidence of conodonts.

SYSTEMATIC DESCRIPTIONS

Numbers with prefix BU refer to the Geology Museum, University of Bristol.

Measurements. The dimensions given apply in every case to the stated diameter. Abbreviations are: *D* = diameter, *U* = umbilical segment of the diameter, *WH* = whorl height, *Wh* = distance from the ventral crest of the whorl to the ventral crest of the preceding whorl, *WW* = whorl width.

Order AMMONOIDEA Zittel 1884

Suborder GONIATITINA Hyatt 1884

Superfamily CHEILO CERATACEAE Frech 1897

Family CHEILO CERATIDAE Frech 1897

Subfamily IMITOCERATINAE Ruzhencev 1950

Genus GATTENDORFIA Schindewolf 1920

Type-species by original designation: *Gattendorfia subinvoluta* Schindewolf 1920.

- 1960 *Gattendorfia* Schindewolf; Vöhringer, pp. 149–50 (see also for earlier references).
 1964 *Gattendorfia* Schindewolf; Gordon, pp. 168–70 (see also for earlier references).
 1964 *Kazakhstania* Librovitch; Gordon, p. 171.
 1965 *Gattendorfia* Schindewolf; Weyer, p. 447.

Gattendorfia sp.

Plate 25, figs. 6–18; text-fig. 3a–e

Material. BU 19635–BU 19666.

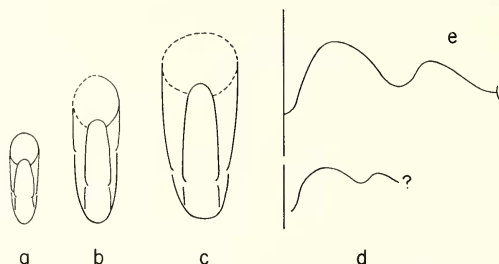
Dimensions (mm.)

	<i>Plate reference</i>	<i>D</i>	<i>U</i>	<i>WH</i>	<i>Wh</i>	<i>WW</i>	<i>Revolutions</i>
BU 19635	Plate 25, figs. 17, 18	c. 6.5	c. 2.5	c. 2.5	c. 2	c. 2	4.5?
BU 19640	Plate 25, fig. 12	5	3	1.3	—	1.5	4.75
BU 19642	Plate 25, fig. 16	4.2	1.8	1.2	—	1.5	4.5
BU 19666	Plate 25, figs. 13, 14	4.2	2	1.2	c. 1.0	c. 1.5	4.5
BU 19637	Plate 25, figs. 7, 8	3.4	1.6	1	0.9	c. 0.9	3.75
BU 19645	Plate 25, figs. 9, 10	2.7	1.05	0.8	c. 0.7	0.7	3
	Gordon (1964, p. 172):	8.5	5.2	2.0	—	2.6	
		9.0	6.4	2.0	—	2.5	
		10.2	7.3	2.2	—	c. 3.0	

Description. Small evolute shells with rounded whorls which are relatively high at early stages of growth. No evidence of external ornament. Whorls each bear two conspicuous constrictions, one succeeded by another at slightly less than half-circumference. Constrictions follow a shallowly sinuous course across the flanks, are so disposed to the axis of growth that their nearest approach to the aperture is on the venter. Suture as in text-fig. 3d, e. External lobe relatively deep.

Remarks. The sutures of these evolute forms have no match among known gattendorfiids. Their character excludes a prolecanitid affinity, and so too does the presence of constrictions. The evolute shell-form and the presence of constrictions are reminiscent of what is seen in the persistently evolute gattendorfiid to which some refer as '*Kazakhstania*'. Librovitch, in 1940, proposed the subgenus *Gattendorfia* (*Kazakhstania*) on the basis of material from central Asia, and suggested it to be distinct from *Gattendorfia* by its evolute form maintained throughout growth. Further, he suggested that *Gattendorfia* (*Kazakhstania*), with its relatively deep, lanceolate external lobe, and with constrictions, need not be confused with the protocanitids, which are also evolute. Miller and Collinson (1951), without discussing the matter, referred to '*Kazakhstania*' as a genus. It was not until 1955 that Miller and Garner proposed that the form be raised to generic rank. They then added an American species to the two described by Librovitch. In 1960 Vöhringer returned these evolutes to synonymy with *Gattendorfia*, and there is much to commend his view. Vöhringer's full analysis of the Hangenbergkalk gattendorfiids has shown how variable are these involution–evolution characteristics of shell form, and it seems good to accept that the continuously evolute shell, which Librovitch saw as the definitive characteristic of his subgenus, is not sufficiently distinctive to justify a relatively elevated systematic position for '*Kazakhstania*'. Certainly, full generic status does not seem justifiable.

Gordon (1964), apparently unaware of Vöhringer's opinion, identified a small, evolute ammonoid from the Mississippian of Arkansas as '*Kazakhstania*? sp.' He suggested that '*Kazakhstania*' might receive also certain small, evolute, constricted ammonoids reported from the Mississippian of Ohio by Hyde (1953). These latter strongly resemble the



TEXT-FIG. 3. *Gattendorfia* sp. a, b, c. Apertural aspect of BU 19645 (terminal diameter 2.7 mm.), BU 19637 (3.4 mm.), BU 19644 (4.3 mm.) respectively. d. Suture of BU 19645 at diameter 1.7 mm. e. Suture (reversed) of BU 19643 at diameter approximately 3.7 mm. (specimen deformed).

individuals encountered in the Cornish fauna (an observation first put to the author by Professor M. R. House).

Weyer (1965), like Vöhringer, regarded '*Kazakhstania*' as synonymous with *Gattendorfia*. Vöhringer, indeed, had gone so far as to suggest that Librovitch's two species were perhaps to be identified with *Gattendorfia tenuis* (a form which ranges through most of the Hangenbergkalk and is still available in the topmost bed, as Vöhringer's table 1 shows). *G. tenuis* is, however, more involute at late stages of growth and must therefore differ from the two forms described by Librovitch. Since Vöhringer found nothing entirely comparable with '*Kazakhstania*' in the Hangenbergkalk there remains a possibility that fully evolute species may be of an age somewhat later than is represented in that sequence. The evidence from the Hangenbergkalk (which has three gattendorfid species still extant in its uppermost part) need not be taken to account completely for the vertical range of *Gattendorfia*. Thus, although these evolute forms lose their generic rank, they may be thought to retain a special stratigraphic interest.

EXPLANATION OF PLATE 25

- Figs. 1, 2. Gen. et sp. nov. A. Right (to display ornament) and left (to display early whorls) views of BU 19668. $\times 8$.
 Figs. 3, 4, 5. Gen. et sp. nov. A. Apertural, lateral and oblique ventral (to display sutures) views of BU 19667. $\times 8$.
 Figs. 6-18. *Gattendorfia* sp. 6, BU 19641. 7, 8, BU 19637. 9, 10, BU 19646. 11, BU 19643 (deformed). 12, BU 19640 (deformed). 13, 14, BU 19666. 15, BU 19638. 16, BU 19642. 17, 18, BU 19635 (deformed). All $\times 8$.



Superfamily GONIATITACEAE de Haan 1825

Family GONIATITIDAE de Haan 1825

Subfamily KARAGANDOCERATINAE Librovitch 1957

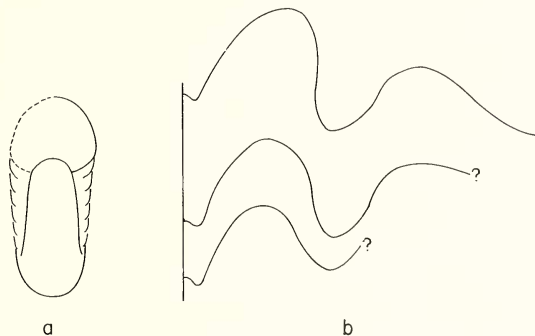
Gen. et sp. nov. A

Plate 25, figs. 1-5; text-fig. 4a, b

Material. BU 19667-BU 19669.

Dimensions (mm.)

	Plate reference	D	U	WH	Wh	WW	Volutions
BU 19667	Plate 25, figs. 3-5	5	1.6	1.8	1.3	2.6	?
BU 19668	Plate 25, figs. 1, 2	4	1.4	1.6	1.1	2.4	3.8



TEXT-FIG. 4. Gen. et sp. nov. A. a. Apertural aspect of BU 19667 (terminal diameter 5 mm.). b. Three successive sutures of BU 19667 at diameters 3.9-4.7 mm.

Description. Narrow, open umbilicus exposes all previous whorls. Whorls depressed, wider than high, maximum width (also overlap) at approximately one-third whorl-height. Ornament of approximately twenty robust umbilical ribs which fade as they curve concave adaperturally beyond the locus of maximum whorl-width and finally approach parallelism with the growth axis. Venter broad, rounded, unornamented. Suture (text-fig. 4b) has broadly splayed external lobe with median saddle.

Remarks. The form reveals its most interesting characteristic in the broad external lobe, with its median saddle. It is therefore a goniatitacean. But like *Karagandoceras* and *Paralytoceras* it has little else in common with the goniatitids.

Weyer (1965), who re-examined *Paralytoceras* and first demonstrated its possession of goniatitacean sutural character, decided to refer both *Karagandoceras* and *Paralytoceras* provisionally to the Karagandoceratinae—this in full awareness of the possibility that the two genera might have arisen along quite independent courses. Weyer preferred to attach the subfamily Karagandoceratinae to the family Goniatitidae, rather than follow Ruzhencev (1962) in identifying a family Karagandoceratidae attached to the Praeglyphiocerataceae. The systematic affiliation of the new genus as given here is

entirely in accordance with Weyer's proceeding: a third genus is added to Karagandoceratinae, and this is done recognizing the possible artificiality of a Gen. et sp. nov. A—*Karagandoceras-Paralytoceras* combination.

The new form has a sutural character sufficient to separate it from any goniatitid of conceivably comparable age, although in its relative robust ornament and in shell-form it appears to be closer to the goniatitids than is *Karagandoceras* or *Paralytoceras*. The resemblance, within the Karagandoceratinae, is more with *Paralytoceras*, especially in the form of the external lobe. The lateral lobes of the two sutures differ slightly, however, and the fimbriate ornament of the more evolute, carinate *Paralytoceras* is altogether different from what is seen in Gen. et sp. nov. A. Certain umbilical ornament is seen among the ammonellipsitids, especially in the young stages of *A. rotuliformis* (Crick) and in *A. homoceratoides* (Schindewolf). In neither case is the exact form of the ornament comparable with what is seen here. The sutures (at much larger diameter) of these two are also different.

Formal proposal and precise diagnosis of the new genus and species is reserved until further, possibly relevant material has been examined. BU 19667 (which was capable of being prepared in order to expose the median saddle) and BU 19668 probably belong to one and the same species. BU 19668 offers no sutural information, but is consistent with BU 19667 in shell-form and ornament. A badly preserved, relatively large third form (BU 19669) has more sharply sculpted ribs than the other two (Pl. 27, fig. 8) and is tentatively referred to the new genus.

Subfamily MUENSTEROCERATINAE Gordon 1964

Genus MUENSTEROCERAS Hyatt 1884

Type species by original designation: *Goniatites oweni* var. *parallela* Hall 1860.

- 1961 *Muensteroceras* Hyatt; Kullmann, pp. 256–8 (see also for earlier references).
- 1961 *Munsteroceras* Hyatt; Pareyn, p. 96.
- 1963 *Muensteroceras* Hyatt; Campbell and Engel, p. 87.
- 1964 *Munsteroceras* Hyatt; Wagner-Gentis, p. 232.
- 1964 *Muensteroceras* Hyatt; Gordon, p. 175 (see also for earlier references).
- 1965 *Dzhaprakoceras* Popov, p. 36.
- 1965 *Muensteroceratoides* Popov, p. 36.

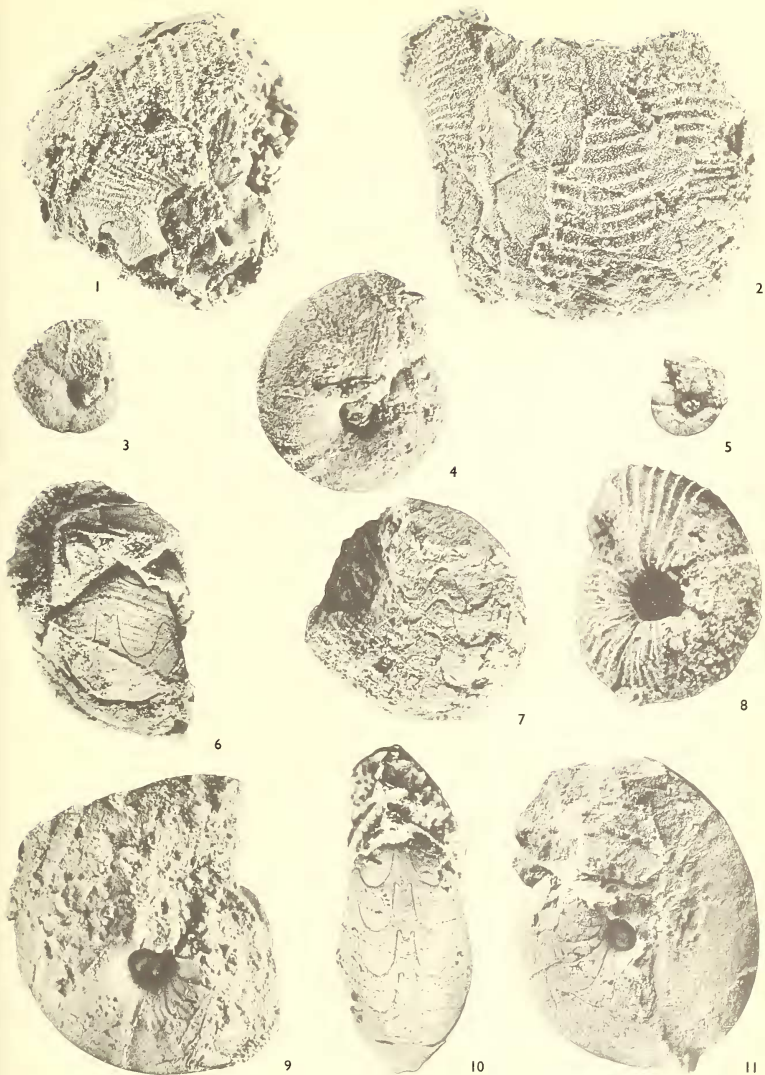
Muensteroceras complanatum (de Koninck 1880)

Plate 26, figs. 10, 11; text-fig. 5c

- 1884 *Goniatites complanatus* de Koninck, p. 106, pl. 46, fig. 4.
- 1940a *Muensteroceras complanatum* (de Koninck); Delépine, pp. 47–52; pl. 3, figs. 3, 4; text-fig. 8.

EXPLANATION OF PLATE 26

- Figs. 1, 2. *Ammonellipsites* sp. indet. Lateral and ventral views of BU 19772. $\times 5$.
- Figs. 3–6, 9. *Muensteroceras* spp. 3, BU 19675. 4, BU 19674. 5, BU 19676. 6, BU 19672. 9, BU 19673. 6×5 , others $\times 8$.
- Fig. 7. *Muensteroceras* cf. *rotella* (de Koninck). Oblique ventral (to display sutures) view of BU 19671. $\times 8$.
- Fig. 8. *Ammonellipsites princeps* (de Koninck). BU 19721. $\times 8$.
- Figs. 10, 11. *Muensteroceras complanatum* (de Koninck). Apertural and lateral views of BU 19670. $\times 5$.



MATTHEWS, Carboniferous cephalopods from Cornwall

Material. BU 19670.

Dimensions (mm.)

	Plate reference	D	U	WH	WW
BU 19670	Plate 26, figs. 10, 11	c. 12	c. 1.0	c. 6.3	c. 4.5
	Delépine (1940a, 47):	65	6-7	33	18

Note. Delépine (1940a, 47) referred in his table to Plate 28, figs. 3 and 4. Obviously, a reference to Plate 27, figs. 3 and 4 was intended.

Remarks. The specimen figured shows well the involution, small umbilicus, high flanks and sutural character (text-fig. 5c) appropriate to this species.

Muensteroceras cf. *rotella* (de Koninck 1880)

Plate 26, fig. 7; text-fig. 5b

Material. BU 19671.

Remarks. One fragment provides evidence sufficient to justify comparison with *Muensteroceras rotella*. The umbilicus appears to be more open than that of *M. complanatum*; the suture line (text-fig. 5b), with a straight-sided external lobe stacked close to the same element of the previous suture line, as is found in *M. rotella*. In this, *Muensteroceras rotella* is close to the American *M. oweni* and *M. parallellum*.

It is worthwhile to note that Delépine (1940a) referred one example of *M. rotella* to a relatively early position in the Tournaisian stratigraphy, and also that an ammonoid collected from the Liegende Alaunschiefer in Germany has been suggested to be identifiable as *M. rotella* (H. Schmidt's opinion, reported in Paproth, Teichmüller and Remy 1960, p. 8).

Muensteroceras spp.

Plate 26, figs. 3-6, 9

Material. BU 19672-BU 19718.

Remarks. Several specimens are referred to the genus *Muensteroceras* on the evidence of their form. Occasionally, sutural evidence is also available. Certain small specimens may carry a hint of faint ribbing (Pl. 26, figs. 4, 9), and some constrictions (Pl. 26, figs. 3, 5).

Subfamily PERICYCLINAE Hyatt 1900
Genus AMMONELLIPSITES Parkinson 1822

Type-species by subsequent designation of Schindewolf 1951b: *Ellipsolithes finatus* Sowerby 1814.

1911 *Pericyclus*; Hind, pp. 107-8; pl. 4, figs. 3, 4, 5, 5a.

1957 *Ammonellipsites* Parkinson; Gordon, pp. 29-33.

1961 *Pericyclus* Mojsisovics 1882 emend. Hyatt 1883; Pareyn, p. 135.

1963 *Pericyclus* Mojsisovics; Campbell and Engel, p. 114.

1964 *Ammonellipsites* Parkinson; Gordon, pp. 172-3 (see also for earlier references).

1964 *Pericyclus* Mojsisovics; Wagner-Gentis, p. 229.

?1965 *Neopericyclus* Popov, pp. 45-6.

Remarks. Gordon (1957) has produced a thorough review of the history of attempts to subdivide this genus. He supplied also a key to recognition of the extant subgenera. Since

present information on the relative ages of the various occurrences of ammonellipsitids is so poor, and since sutural evidence is not available in every case, there is a danger that these subgeneric associations of ammonellipsitid species may be artificial and phylogenetically uninformative. No subgeneric assignments are made here.

Ammonellipsites princeps (de Koninck 1844)

Plate 26, fig. 8; Plate 28, figs. 1–7; text-fig. 5a

1844 *Ammonites princeps* de Koninck, pp. 579–80; pl. 51, figs. 2a, b, c, 3a, b, c (de Koninck's publication is given the dates 1842–4. Delépine (1940a) refers to Koninck's proposal of *Ammonites princeps* to the year 1842).

1940a *Pericyclus princeps* (de Koninck); Delépine, pp. 38–40; pl. 1, figs. 12–15; text-fig. 7 (see also for earlier references).

Material. BU 19719–BU 19761.

Dimensions (mm.)

	Plate reference	D	U	WH	Wh	WW	No. of ribs
BU 19719	Plate 28, figs. 1, 2	c. 6·8	1·3	c. 3·4	c. 2·6	4·8	c. 60
BU 19720	Plate 28, fig. 7	c. 10·0	c. 2·0	c. 4·0	?	6·8	
BU 19721	Plate 28, fig. 6	c. 5	1·2	1·8	c. 2·0	3·2	c. 50
BU 19723	Plate 28, fig. 5	3·3	1·0	1·4	?	2·8	c. 40
BU 19726	Plate 28, fig. 3	2·2	0·7	0·8	?	1·4	—
	Delépine (1940a, 39):	35	10	—	—	—	42
	„	34	11	—	—	—	> 50

Remarks. BU 19719 shows well the sutural (text-fig. 5a) and sculptural characteristics of the species, although ribs may be more numerous than in the larger Belgian specimens. Other specimens (BU 19720–BU 19761), if their ornament is well preserved, may also be referred to this species. Some further small individuals possibly fit to be compared with *A. princeps* are included in *Ammonellipsites* spp. (below).

The relatively robust ribs curve convex-adapically across the venter, but their curvature is always more slight than in the American form *A. blairi*. Occasional instances of bifurcation are seen. The constrictions, up to four in number per whorl, are relatively broadly developed, and their course parallels that of the ribs.

Ammonellipsites sp. aff. *asiaticus* (Librovitch 1940)

Plate 27, figs. 5, 9, 10

1940 *Pericyclus asiaticus* Librovitch, pp. 122–30, 268–72; pl. 16, figs. 1–6; pl. 17, figs. 1–4; text-figs. 43–51.

1940 *Pericyclus asiaticus* var. *simplex* Librovitch, pp. 130–1, 272; pl. 17, figs. 5, 6; text-figs. 52, 53.

EXPLANATION OF PLATE 27

Figs. 1–4, 6, 7. *Ammonellipsites* spp. 1, 2, BU 19730 (cf. *A. princeps*). 3, BU 19724 (cf. *A. princeps*). 4, BU 19766 (cf. *A. sp. aff. asiaticus*). 6, BU 19729 (cf. *A. princeps*). 7, BU 19765 (cf. *A. sp. aff. asiaticus*). All $\times 8$.

Fig. 8. Gen. et sp. nov. A? BU 19669. $\times 5$.

Figs. 5, 9, 10. *Ammonellipsites* sp. aff. *asiaticus* (Librovitch). 5, BU 19764. 9, 10. Lateral and ventral (to display spiral ribbing) views of BU 19762. 5, $\times 8$, others $\times 5$.



1



2



3



4



5



10



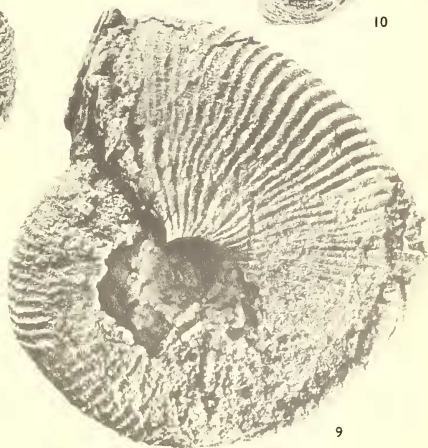
6



7



8

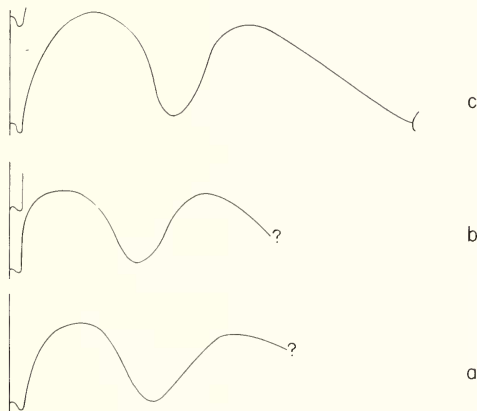


9

Material. BU 19762-BU 19771.

Dimensions (mm.)

	Plate reference	D	U	WH	Wh	WW
BU 19762	Plate 27, figs. 9, 10	17	2.4	8	5.3	9
BU 19763		c. 16	c. 1.2	c. 10.5	6	c. 7.5
BU 19764	Plate 27, fig. 5	7.7	0.6	4	2.6	c. 5.8
?BU 19766	Plate 27, fig. 4	4.7	0.6	2.0	?	c. 3.6
?BU 19765	Plate 27, fig. 7	3.8	0.5	1.8	c. 1.4	c. 2.4



TEXT-FIG. 5. *a.* *Ammonellipsites princeps*. Suture of BU 19719 at diameter 4.5 mm. *b.* *Muensteroceras* cf. *rotella*. Suture of the incomplete specimen BU 19671, with ventral element of the succeeding suture shown. *c.* *Muensteroceras complanatum*. Suture of BU 19670 at diameter 10 mm., with ventral element of the succeeding suture shown.

Description. The shell is tightly involute and the narrow umbilicus has a rounded margin. The last whorl is relatively high, with extensive flanks and a rounded venter. On the largest specimen (terminal diameter 17 mm.) approximately eighty ribs can be counted on the venter. The fine ribs increase by bifurcation, and rarer intercalation, achieved near the locus of maximum whorl-width. Of the two secondary ribs produced by bifurcation one is immediately collinear with the primary rib and the other diverges adapically. The ribs follow a sinuous course across the flanks with a weak, broad, adaperturally concave curve whose turning-point is situated near half whorl-height. There is a clear ventral sinus. In addition to these transverse sculptural elements a minor spiral set is present, best seen in troughs between major ribs. The spiral elements are collinear in adjacent troughs. Interference of transverse with spiral sculptural elements results in a serrate condition seen in the better-developed transverse ribs. There are no constrictions. The suture is unknown.